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DEVELOPMENT OF A SOLDIER
Of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) AND ITS PHYLOGENETIC SIGNIFICANCE*[1]

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(Figs. 24–32 incl.)

OUTLINE

Introduction

During my studies on the life of termites at Kartabo, British Guiana, I happened, by chance, to find a molting termite in a nest of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) (Fig. 26) which appeared to be a nasuate soldier emerging from a pigmented worker skin. I had been carefully searching the nest for a remarkable termitophilous Staphylinid, *Spirachtha,* but realizing the significance of my chance discovery, I continued to hunt for molting individuals. Altogether, during my studies in British Guiana, I found about six specimens, most of which (Fig. 27, *b*) were in the middle of the process. In addition to these molting specimens, I fixed a large number of workers, soldiers and nymphs of this species in Bouin-Dubose, Gilson's, Hot Corrosive Sublimate and Alcohol. This

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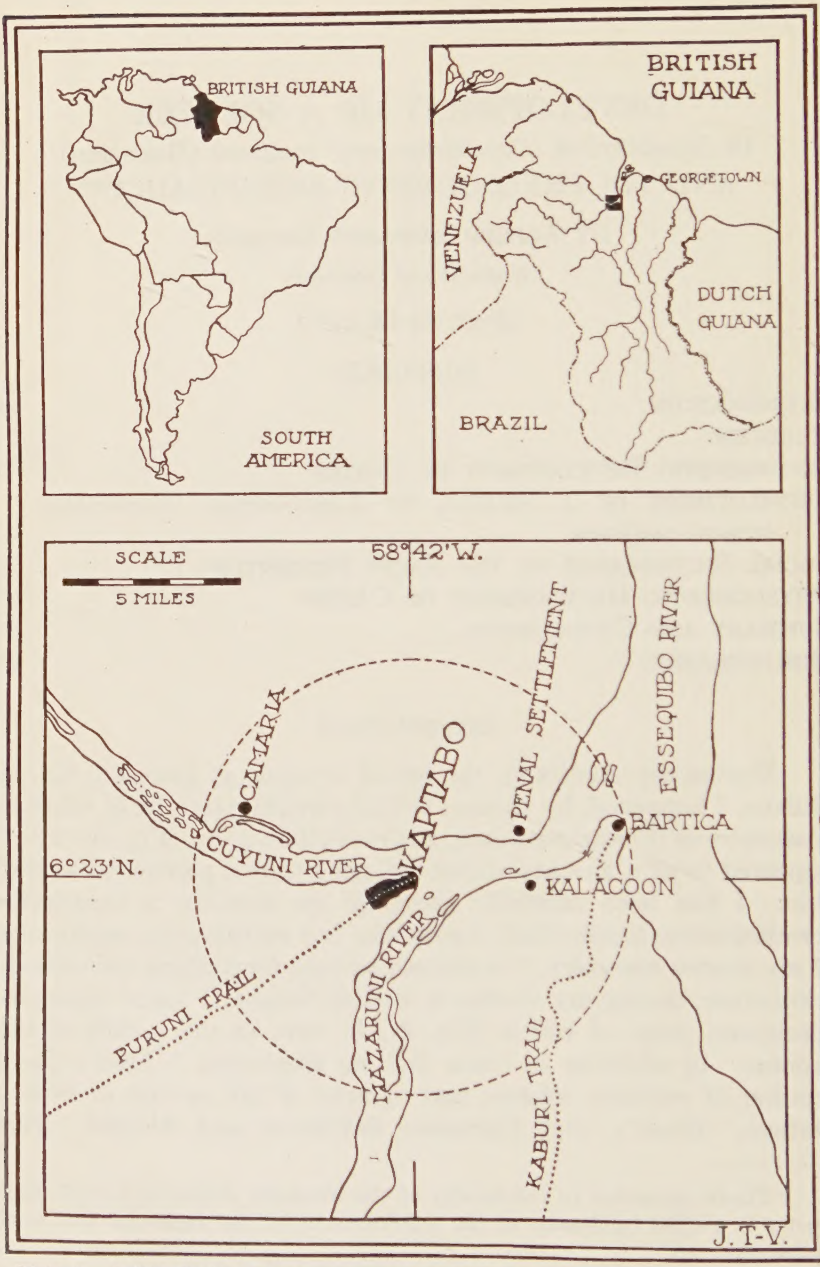


Plate A. British Guiana Tropical Research Station of the New York Zoological Society. Circle represents a radius of six miles.

material forms the basis of this report. About twenty insects were sectioned and stained, making about sixty slides.

The work has been done under the direction of Dr. O. A. Johannsen of Cornell University to whom I am immensely indebted for his advice and suggestions. I wish also to take this occasion to thank Professor H. D. Fish of the University of Pittsburgh for his interest in this problem and for the many hours in which we discussed various theories to account for the facts presented. I am also indebted to Dr. Caroline B. Thompson and Dr. T. E. Snyder for their interest and valuable suggestions. It was my great misfortune not to be able to personally talk over the problem with Dr. Thompson before her untimely death in December 1921.

Problem

My purpose has been to answer the following questions related to the discovery of the molting individuals:

1. What is the caste of the individual before it molts? Is it a true worker, or can it be distinguished from the true worker?
2. What are the internal and external changes which take place during this metamorphosis?
3. In what way does this metamorphosis help to explain the phylogenetic development of the castes in question?

Ontogenetic Development of Castes

Many writers, particularly the early students of polymorphism among the social insects, have believed that food was either a direct cause of caste production or else served to stimulate or inhibit the development of the different castes from undifferentiated young.

The observations of the following authors, historically reviewed by Thompson (1917) have supported this hypothesis: Lespès (1856), Müller (1873–75), Weismann (1892, 1893, 1894, 1902), Spencer (1893–94), Grassi and Sandias (1893–94), Emery (1893, 1896, 1904, 1910), Silvestri (1902, 1903), Desneux (1904), Escherich (1909), Holmgren (1909) and Feytaud (1912). Jucci (1920, 1924, 1925) also supports this theory.

The belief that the intestinal protozoa influence caste production in termites was advanced by Grassi and Sandias (1893–94). This theory has been completely refuted by the work of Imms (1919) and Cleveland (1923, 1923a, 1924, 1925, 1925a, 1925b).

The following authors have contributed to the belief that the castes are already predetermined at the time of hatching and are not due to food or its influence:

Bobe-Moreau (1843) states that he was able to distinguish soldier nymphs among newly hatched forms. This is probably an erroneous observation.

Hagen (1855–60) quotes Bates, who was then in Brazil, as saying that he believed that the castes were not undifferentiated at the time of hatching, but that the sexual forms were distinct from the others. His belief lay, not in observing any differences in the newly hatched nymphs, but in the fact that all types were found in the nests together in the same cells, and that it seemed unlikely that special food could be administered to any particular group.

Dewitz (1878) believes that the eggs must be predetermined within the body of the mother.

Knower (1894) observed the molt from a worker-like nymph into a nasuate soldier in a species of *Nasutitermes* determined later by Banks as *N. pilifrons*. Knower found a nymph with 13 antennal segments, which was worker-like in its head and jaws, but possessed a small frontal gland. This form molted into a nasuate soldier.

Wheeler (1907) makes the following statement with regard to ants.

"While experiments on many organisms have shown that the quality of assimilated food may produce great changes in size of stature, there is practically nothing to show that even very great differences in the quality of the food can bring about morphological differences of such magnitude as those which separate the queens and workers of many ants.

". . . . It must be admitted that a direct causal connection between underfeeding on the one hand and the ontogenetic loss or development of characters on the other, has not been satisfactorily established. The conditions in the termites, which are often cited as furnishing proof of this connection, are even more complicated and obscure than those of the social Hymenoptera."

Bugnion (1912a) states that he found an individual, 1.3 mm. long, with a distinct frontal projection, frontal gland and duct, among a number of newly hatched nymphs of "*Eutermes*" (= *Nasutitermes*) *lacustris*. In correspondence with Miss Thompson, however, he writes that he now believes that he was mistaken. He very likely mistook the long labrum for the nose, which it resembles in the early stages, and confused the frontal gland with the brain (Thompson, 1919).

Snyder (1915) observed and figured the change from worker-like nymphs to soldiers. He makes the following statement with regard to *Reticulitermes flavipes* and *R. virginicus:*

"In the development of the soldier, however, marked changes in form occur, the mature soldier, with pigmented head and saber-like mandibles, being developed from a large-headed, white, worker-like larva."

Thompson (1917), in commenting upon this observation of Snyder's, says:

"This fact proves for *Leucotermes* (= *Reticulitermes*), as Knower's work did for *Eutermes* (= *Nasutitermes*), that the worker-like nymph from which the soldier develops resembles the worker in external characters only, but internally possesses the distinctive organs of the soldier caste."

In my opinion, Thompson's (1917) paper on the origin of castes in *Reticulitermes* stands out as the most important work on this problem which has yet been done. She traces the development of species of this genus very carefully from their emergence from the egg. Her summary at the end of the paper is as follows:

"1. The newly hatched nymphs of *L. flavipes* and *L. virginicus* are externally all alike, but internally there are marked structural differences which divide the nymphs into two sharply defined types, the reproductive and the worker-soldier types, which are respectively the prototypes of the 'small headed' and 'large headed' nymphs of Grassi. Therefore, the fertile and sterile types are predetermined at the time of hatching.

"2. The two types of newly hatched nymphs may be distinguished by the following characters: a, the bulk of the brain; b, the relative size of brain and head; c, the structure of the compound eyes; and d, the size of the sex organs.

"3. The reproductive type of newly hatched nymph has a large brain, in which the mushroom bodies, optic lobes and antennary lobes are all large. The space within the hypodermis of the head is nearly filled by the brain. The compound eyes are slightly larger and more differentiated, and the sex organs are larger than in the worker-soldier type.

"4. The worker-soldier type of newly hatched nymph has a small brain, with small mushroom bodies, optic lobes and antennary lobes. The space within the hypodermis of the head is not nearly filled by the brain. The compound eyes are smaller and simpler, and the sex organs are smaller than in the reproductive type.

"5. The antennae of the newly hatched nymphs of both *L. flavipes* and *L. virginicus* are composed of nine segments, the third segment grooved and bare.

"6. In nymphs of *L. flavipes* with ten antennary segments, the third segment grooved, and a body length of 1.3 to 1.4 mm., the individuals of the reproductive type are further differentiated into two groups: a, with large brain and large sex organs; b, with slightly smaller brain and smaller sex organs.

These are the respective prototypes of the nymphs of the first form and the nymphs of the second form, and hence of the two adult castes of the first form, with long wings, and of the second form, with short wing pads.

"7. The prototypes of the worker and soldier castes, although externally alike, are distinguishable by internal structures at the end of the second stage of development, in nymphs with a body length of 3.75 mm., and are probably distinguishable at an even earlier age.

"8. The frontal gland is present, although barely recognizable, in the newly hatched nymphs, and grows larger and more complex as development proceeds. The fontanelle nerve (median ocellar nerve) is not present in the earlier phases, but is clearly seen in individuals with a body length of 1.6 mm. From the beginning, the frontal gland is larger and more differentiated in individuals of the reproductive type than in the worker-soldier type, and may be added to the list of characters by which the two types are distinguished. In individuals of the large headed worker-soldier type, with a body length of 3.75 mm. two types of frontal glands may be recognized: a small, primitive frontal gland in the worker prototypes, a large, highly modified gland in the soldier prototypes.

"9. No evidences of a prototype for the third adult reproductive caste, without wing pads, have been seen in this study of the development of *L. flavipes*.

"10. To simplify the heterogeneous nomenclature of the three adult reproductive castes I have suggested the following terms, which are in conformity with the terms applied to the oldest nymphs since the time of Lespès (1856):

1. Adults of the first form, or males and queens of the first form (with long wings or stubs of wings).
2. Adults of the second form, or males and queens of the second form (with short wing pads).
3. Adults of the third form, or males and queens of the third form (with no wing pads)."

In another paper, Thompson (1919) continues this study on other genera and species of termites with the same general conclusions. The work on a species of *Nasutitermes* (*N. pilifrons*), called *Eutermes* in the paper, is of particular interest in connection with the observations which I am presenting in the following pages. *Nasutitermes pilifrons* belongs to the subgenus *Nasutitermes* s. str. and is not very closely related to the species of the subgenus *Constrictotermes*. Miss Thompson's observations are as follows:

"*E.* (= *Nasutitermes*) *pilifrons* like all the other termites described in this paper, has the two types of newly hatched nymphs which are alike in external structure:—the reproductive nymphs with a large brain and large sex organs, and the worker-soldier nymphs, with smaller brain and smaller sex organs. . . .

"In worker-soldier individuals about 2 mm. long and with twelve antennal segments there is as yet no external differentiation between the two sterile castes, but an internal differentiation has already begun and may be observed in

whole mounts of stained individuals as well as in sections. The future soldiers are distinguishable by the presence of the larger frontal gland which appears, in frontal mounts of the head, as a small dense spot posterior to the brain; in whole mounts of the head of the future worker no such spot is visible. After examining the stained specimens in cedar oil to separate the future soldiers from the future workers, the two kinds of individuals were embedded and sectioned. In the soldier nymphs a large, although embryonic, frontal gland opens to the exterior on the frontal surface of the head. This gland was more than three times the size of the vestigial gland found in the worker nymphs.

"The soldier caste of *E. pilifrons* is, therefore, not differentiated by external characters at the time of hatching, but arises later in development, being first manifested in individuals about 2 mm. long with twelve antennal segments. The worker caste is differentiated at the same time, and the two castes may be recognized by the size and structure of the respective frontal glands; although no external differentiations are yet present in either caste.

"The differentiation of the worker-soldier nymphs of *E. pilifrons* into the worker and the soldier is nearly parallel with the development of these two castes from the worker-soldier form in the genus *Reticulitermes*, the chief difference being the age of the respective nymphs, the differentiation being visible in *E. pilifrons* in nymphs 3.75 mm. long, although, from the maturity of the frontal gland, it could probably be seen in an earlier phase."

Imms (1919) also believed that nutrition could not be a causal factor in producing polymorphism in termites and indicated his strong belief in intrinsic factors which predetermined the caste in the egg.

Snyder (1925) brings many biological facts together to disprove the theory that food can influence caste production.

It is the writer's opinion that the careful work of these authors, particularly that of Miss Thompson, strongly indicates that all termite castes are predetermined in the egg.

Development of a Soldier of *Nasutitermes* (*Constrictotermes*) *cavifrons*

The case described in the following pages differs from the development already referred to by Knower (1894) and Thompson (1917, 1919) in that the nasuate soldier molts from a fully pigmented form which not only resembles the normal mature worker, but functions as such in the social life of the colony. The worker-like nymphs formerly described were either white or else only slightly pigmented, and it has never been thought, as far as I am aware, that they functioned as workers except in the case of the *Kalotermitidae*.

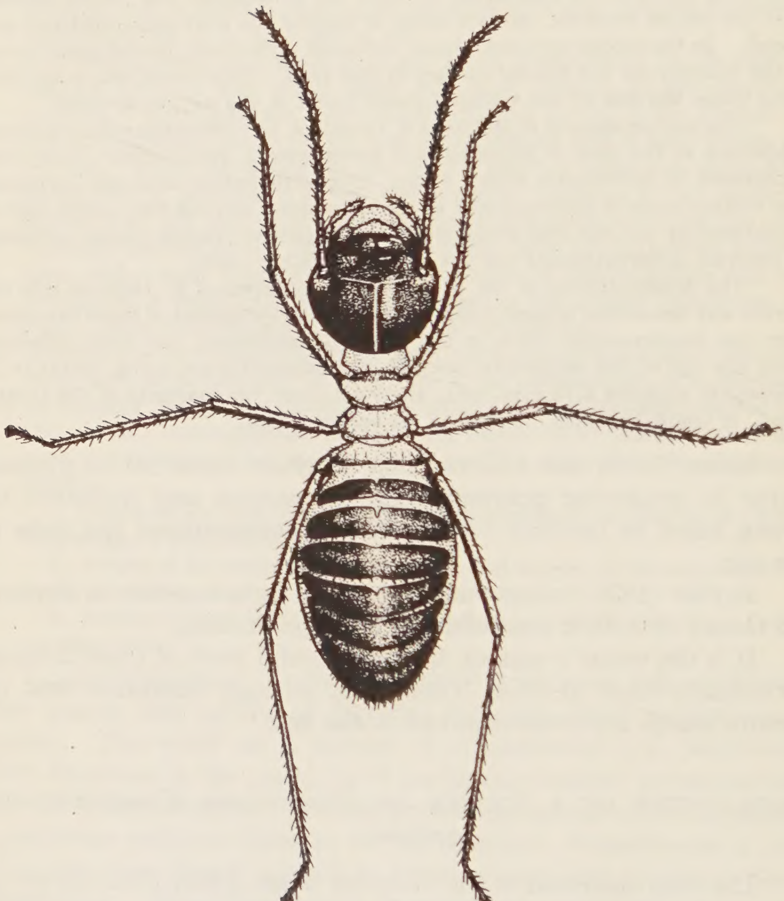


Fig. 24. Small pigmented, work-like form of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) which later changes into a soldier.

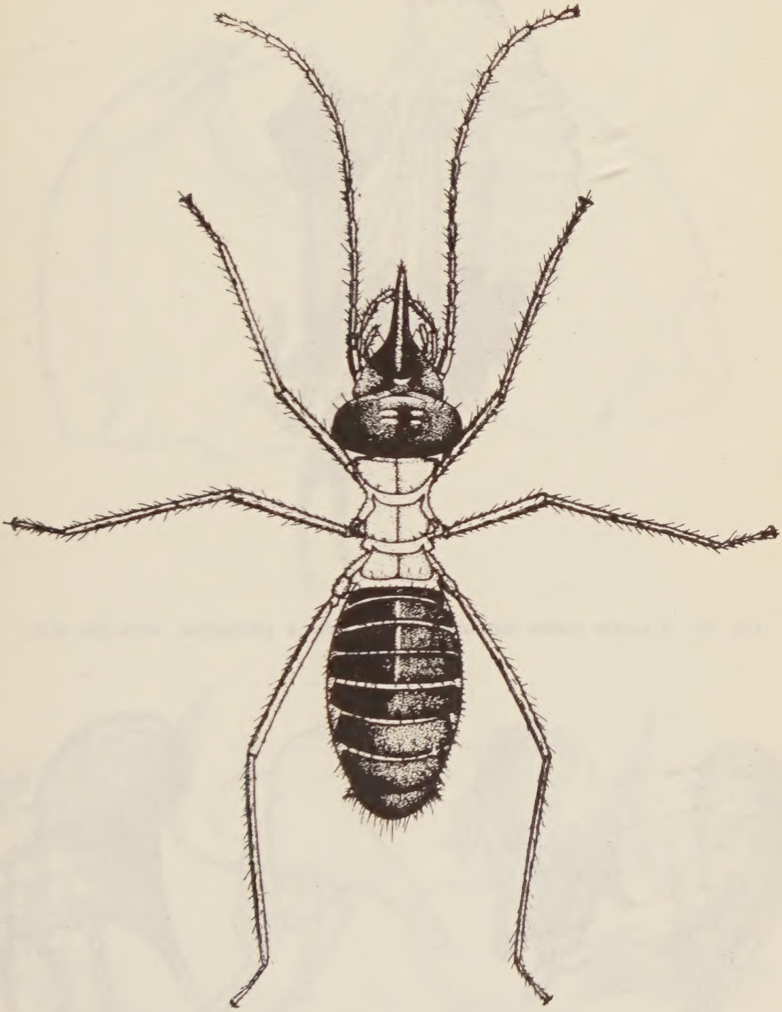


Fig. 25. Mature, pigmented soldier of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren).

Fig. 26. Nasuate soldier nymph emerging from a pigmented, work-like skin.

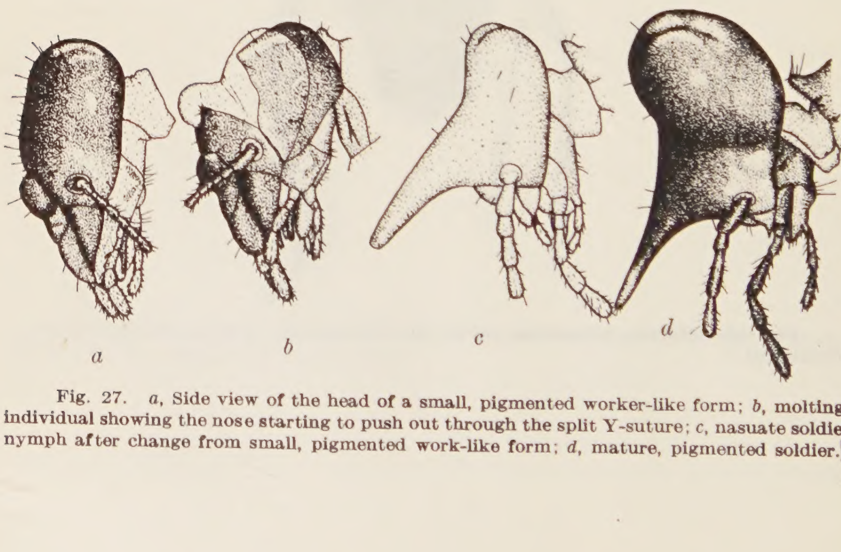
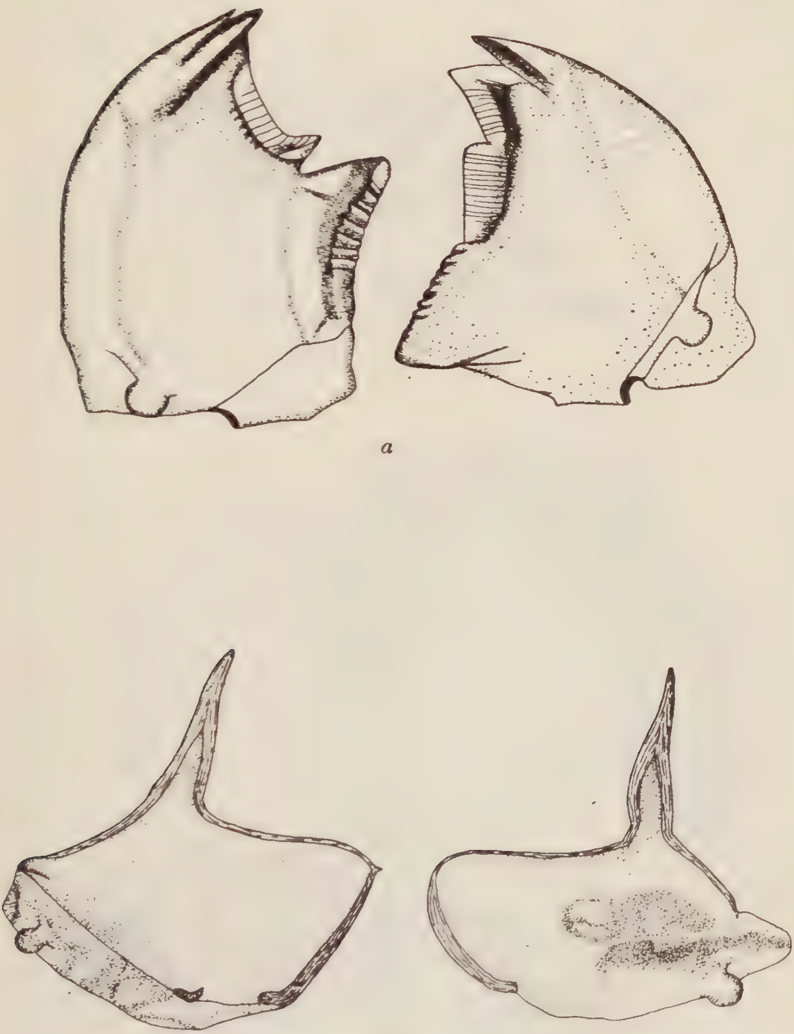


Fig. 27. *a*, Side view of the head of a small, pigmented worker-like form; *b*, molting, individual showing the nose starting to push out through the split Y-suture; *c*, nasuate soldier nymph after change from small, pigmented work-like form; *d*, mature, pigmented soldier.]



a

b

Fig. 28. *a*, Mandibles of a small, pigmented, worker-like form; *b*, mandibles of a mature, pigmented soldier.

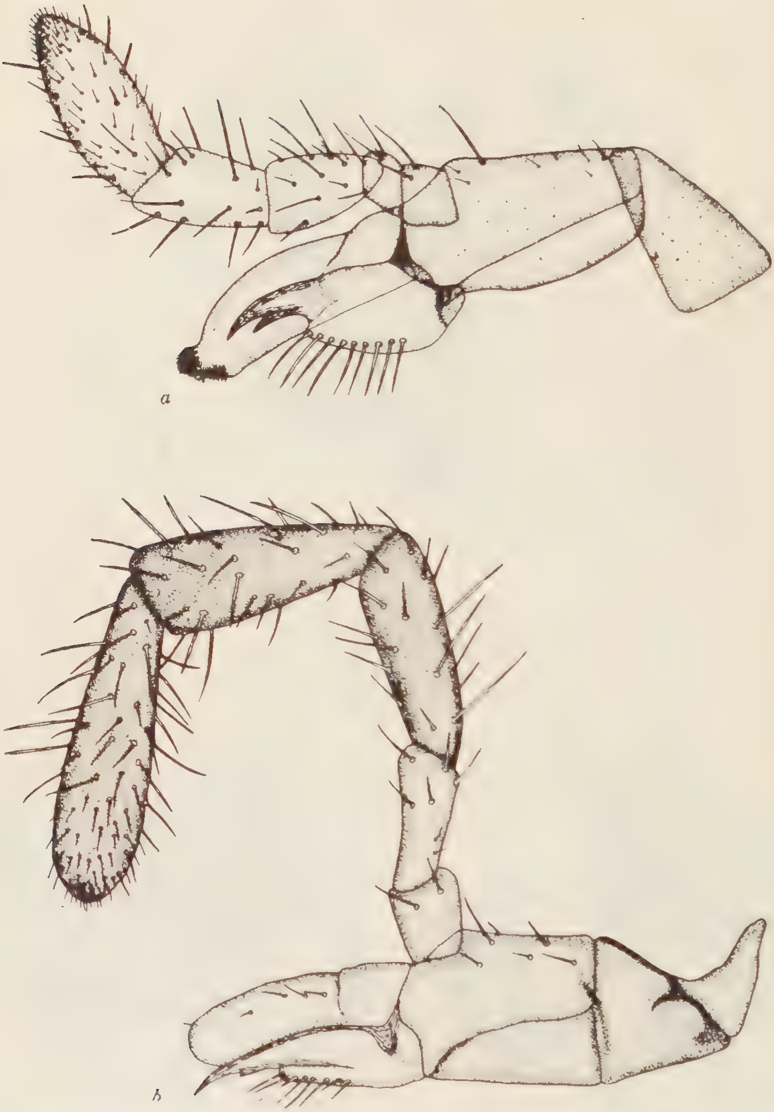
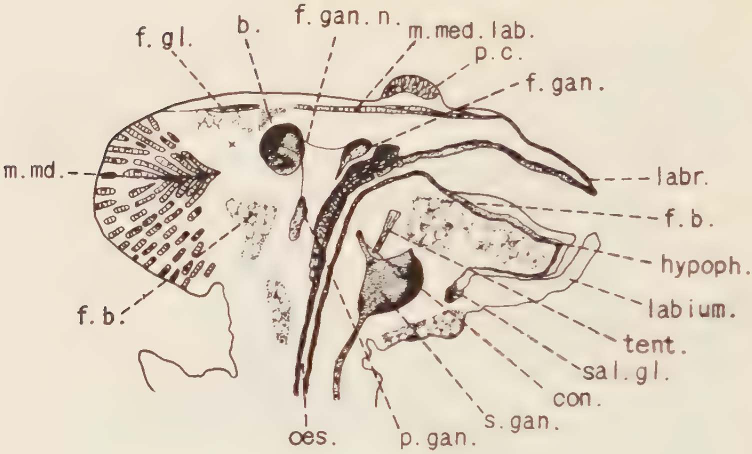
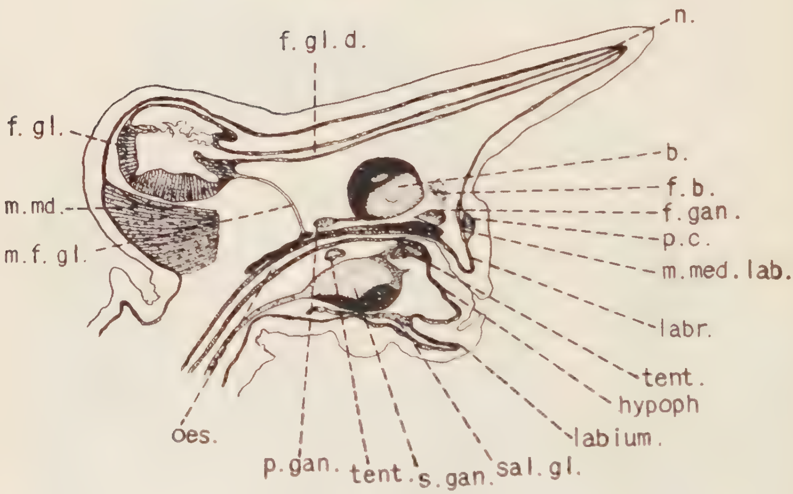


Fig. 29. *a*, Maxilla of a small, pigmented, worker-like form; *b*, maxilla of a mature, pigmented soldier.

Fig. 30. *a*, Labium of a small, pigmented, worker-like form; *b*, Labium of a mature, pigmented soldier.



a



b

Fig. 31. *a*, Longitudinal section through the head of a small, pigmented, worker-like form; *b*, Longitudinal section through the head of a soldier nymph. The development of the frontal gland and the presence of an outer chitinous sheath indicates that this specimen was soon to molt into a mature soldier; *b*, brain; *con.*, connective; *f.b.*, fat body; *f. gan.*, frontal ganglion; *f.gan.n.*, frontal ganglion nerve; *f.gl.*, frontal gland; *f.gl.d.*, frontal gland duct; *hypoph.*, hypopharynx; *labium.*, labium; *labr.*, labrum; *m.md.*, *m.* adductor mandibulae; *m.med.lab.*, *m.* retractor labri medialis; *m.f.gl.*, muscle of the frontal gland; *n.*, nose; *oes.*, oesophagus; *p.c.*, posterior clypeus; *p.gan.*, posterior ganglion of the oesophageal sympathetic system; *sal.gl.*, salivary gland; *s. gan.*, suboesophageal ganglion; *tent.*, tentorium.

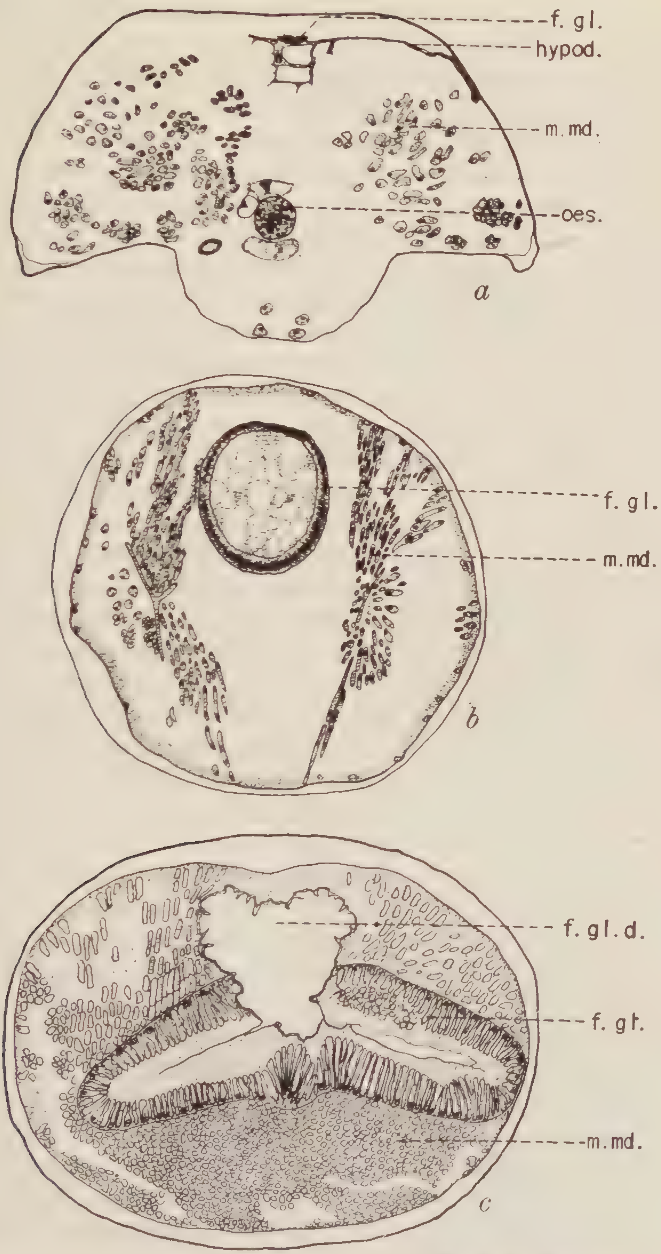


Fig. 32. *a*, Cros-section through the head of a small, pigmented, worker-like form in the region of the frontal gland; *b*, cross-section through the head of a recently emerged soldier nymph in the region of the frontal gland; *c*, cross-section through the head of a mature pigmented soldier in the region of the frontal gland; *f.gl.*, frontal gland; *f.gl.d.*, frontal gland duct; *hypod.* hypodermis; *m. md.*, *m.* adductor mandibulae; *oes.*, oesophagus.

At first I was unable to detect any external difference between the adult workers and the forms which were to molt into soldiers. However, upon careful measurement of head widths of 100 workers and worker-like forms, I found that I could distinguish two groups which never overlapped, one large headed group with head widths from .936 mm. to 1.032 mm. and one small headed group with head widths from .839 mm. to .887 mm. These were further seen to vary slightly in the appearance of the fontanelle, or plate marking the opening of the frontal gland. The smaller type had a somewhat larger and more distinct fontanelle than the larger type. Upon careful measurement, I found that all the molting individuals were coming from the skins of the smaller of the two types. I therefore assume, although it is admitted that the number of molting forms is not enough to be certain, that the soldier develops from the smaller of the two types of pigmented workers. Sections of these types also show a slight difference in the development of the frontal gland, the smaller form having the larger gland. In both cases, however, the gland is very small and difficult to find in the sections and may be considered to be in an embryonic, non-functional state.

The small worker-like form (Fig. 24) differs considerably from the mature soldier (Fig. 25) however. The pigmentation is almost the same in these forms and also in the mature worker. The head of the soldier is prolonged into a "nose" through which a duct (Fig. 31, *b*) runs for the purpose of conducting the fluid secreted by the frontal gland to the surface. The mandibles of the soldier (Fig. 28, *b*) are rudimentary and non-functional. The antennae of the soldier (Fig. 25) are longer than those of the worker-like form (Fig. 24) and consist of 15 segments instead of 16 as found in the worker-like form. Other differences which are not so apparent will be discussed under the changes which take place during the molting.

No frontal process is present in the worker-like form (Fig. 27, *a*) and the mandibles (Fig. 28, *a*) are toothed and functional, being used for cutting wood. They resemble those of the imago in appearance. At the time of molting the individual becomes inactive, lies on its side with its head bent down, and does not move. The integument splits along the Y-suture in the head (Fig. 27, *b*), and along the dorsal side of the thorax and the first few abdominal segments (Fig. 26). The nose starts to grow out (Fig. 27, *b*) until it gets quite long (Fig. 27, *c*). As the skin is shed the emerging individual assumes the shape of the solider nymph.

The soldier nymph emerging from the worker-like skin is white, the posterior portion of the head is not enlarged as it is in the mature soldier (Fig. 27, *d*), the nose is stouter and the frontal gland (Fig. 32) is not yet fully developed. I feel certain, although I found no specimens molting from this stage to the mature soldier type, that there is yet another molt before the final form is reached. Of the many soldier nymphs observed with the developed nose, all were of this shape or else were of the exact type of the mature soldier except that they lacked pigmentation to a considerable extent. No intermediate types were found which would have been the case had the nymph, emerging from the worker-like stage, assumed the shape of the mature soldier gradually without another molt. The soldier nymph illustrated in Fig. 31, *b* shows the stage just before the final molt.

The mature soldier (Fig. 27, *d*) is quite different in shape from the nymph just described (Fig. 27, *c*). The head bulges in back and a section shows the frontal gland has enormously developed (Fig. 32, *c*). The nose is more slender.

That the frontal gland develops gradually while in the stage of the soldier nymph is apparent from the longitudinal section of one of these nymphs (Fig. 31, *b*) which shows a more highly developed gland than that shown in cross-section (Fig. 32, *b*), although the two specimens were alike in external appearance.

The antennae, mandibles, maxillae and labium of the soldier nymph as it emerges from the worker-like skin, are essentially the same as those of the mature soldier except that they are not chitinized and are not as compact as their final form (Fig. 28, *b;* Fig. 29, *b;* Fig. 30, *b*).

It is interesting to note that one segment of the antenna is lost during this process. In all other cases of which I am aware, the antennae, if anything, add segments during the molt. In this case, I believe that the third and fourth antennal segments of the worker-like form fuse into one.

In addition the segments of the antennae become longer and, correlated with this, the maxillary palpi and labial palpi become much elongated (Figs. 29–30).

A summary of these changes follows:

1. The head prolongs itself into a long "nose" from a flat surface, the end of the nose corresponding to the fontanelle plate in position at the junction of the Y-suture (Fig. 27, *a-b*).

2. The antennae each lose one segment, probably through the fusion of the 3d and 4th segments of the worker-like form, and in addition the antennal segments elongate.
3. The mandibles change from large toothed types to reduced non-functional small points (Fig. 28).
4. The maxillae lose the hairy end of the galea and the palpi become much elongated (Fig. 29).
5. The labium changes in shape, the submentum growing longer side projections and the palpi elongating (Fig. 30).

Internally other changes take place.

6. The frontal gland develops from a small inconspicuous organ composed of modified hypodermis (Fig. 32, *a*) into a large sac rounded in outline (Fig. 32, *b*) and later, in the soldier nymph, it becomes further differentiated with two side lobes (Fig. 32, *c*).
7. A duct develops from the hypodermis running to the end of the nose which, in the mature soldier, is hard and ridged on the inside (Fig. 31, *b;* Fig. 32, *c*).
8. The frontal gland muscle (Fig. 31, *b*) enlarges and becomes functional. I have not seen this muscle in sections of the workers and worker-like forms, but Holmgren (1909) illustrates it in the head of an imago of *Nasutitermes*.
9. The muscle situated medially from above the brain to the labrum, *the m. retractor labri medialis* (Fig. 31), becomes very much reduced in the soldier.
10. The *m. adductor mandibulae*, becomes more compact and probably becomes non-functional (Figs. 31–32).

Social Significance of the Facts Presented

The facts outlined seem to indicate that this termite has a specialized, worker-like soldier nymph which functions as a worker in the colony. The contents of the intestines of these worker-like forms indicated that they gathered sand and wood in no way different from the actions of the mature worker. At different times I observed both types of workers carrying sand to their nest and in the nest both seemed to function alike in the care of the queen and other members of the colony.

After passing through this pigmented, functional worker stage, they again become soft, unpigmented and dependent upon the other forms for food. After passing through the unpigmented,

nasuate soldier nymph stage and again molting, the same individual assumes the function of defense in the colony with the use of the now functional frontal gland secretion. The soldier is now unable to feed itself or to carry on any of the specialized activities of its former life.

Is not this change nearly as remarkable as that found in the insects with complete metamorphosis?

The only parallel case I know among termites is that of the nymphs of the reproductive and soldier castes of the *Kalotermitidae*. Here we find nymphs again carrying on the worker functions and later, as far as is known, molting and developing into soldiers or reproductive forms. We are reasonably sure that there is no worker caste among the *Termopsinae*, *Stolotermitinae* and *Kalotermitinae* (Imms, 1919; Thompson, 1919, 1922).

Phylogenetic Development of Castes

Little is known of the phylogenetic origin of the termite castes, nor do we know any facts that might lead to an explanation of their occurrence such as determining factors in the chromosomes. We are not even sure whether they have developed after the origin of social life or whether something analogous to the castes might not have existed before, such as we find in the wingless and winged states of certain Homoptera, Heteroptera and Zoraptera. No fossils exist which might be of assistance in solving this problem, so we are forced to draw our conclusions from the linear series presented by living termites.

Many biologists have found the evolution of polymorphism among social insects fertile ground for speculation. I believe that a brief historical review will serve to focus our attention upon the significance of the facts known and thus cause greater activity in the search for new facts.

Darwin (1859) in the 'Origin of Species' states:

"The subject well deserves to be discussed at great length, but I will here take only a single case, that of working or sterile ants. How the workers have been rendered sterile is a difficulty; but not much greater than that of any other modification of structure. . . . But I must pass over the preliminary difficulty. The great difficulty lies in the working ants differing widely from both the males and the fertile females in structure, as in the shape of the thorax, and in being destitute of wings and sometimes of eyes, and in instinct. . . . According to M. Verlot, some varieties of the double annual stock from having been long

and carefully selected to the right degree, always produce a large proportion of seedlings bearing double and quite sterile plants. These latter, by which alone the variety can be propagated, may be compared with the fertile and female ants, and the double sterile plants with the neuters of the same community. As with the varieties of the stock, so with social insects, selection has been applied to the family, and not to the individual, for the sake of gaining a serviceable end."

Weisman also held this view of the phylogenetic origin of termite castes (1893, 1894). In a later book (1909), he makes the following statement:

"If we regard the variation of the many determinants concerned in the transformation of the female into the sterile worker as having come about through the gradual transformation of the ids into worker-ids, we shall see that the germ plasm of the sexual ants must contain three kinds of ids, male, female, and worker-ids, or, if the workers have diverged into soldiers and nest-builders, then four kinds. We understand that the worker-ids arose because their determinants struck out a useful path of variation, whether upwards or downwards, and that they continued in this path until the highest attainable degree of utility of the parts determined was reached. But, in addition to the organs of positive or negative selection-value, there were some which were indifferent, as far as the success, and especially the functional capacity of the workers, was concerned; wings, ovarian tubes, *receptaculum seminis*, a number of the facets of the eye, perhaps even the whole eye. As to the ovarian tubes it is possible that their degeneration was an advantage for the workers in saving energy, and if so, selection would favour the degeneration; but how could the presence of eyes diminish the usefulness of the workers of the colony? or the minute *receptaculum seminis*, or even the wings? These parts have therefore degenerated because they were of no further value to the insect. But if selection did not influence the setting aside of these parts because they were neither of advantage or disadvantage to the species, then the Darwinian factor of selection is here confronted with a puzzle which it cannot solve alone, but which at once becomes clear when germinal selection is added. For the determinants of organs that have no further value for the organism, must, as we have already explained, embark on a gradual course of retrograde development."

Wheeler (1917) makes the following statement:

"In most species of ants the constant and striking structural differences between the different castes would, at first sight, suggest that such forms as the apterous females, apterous males, soldiers and workers, must have arisen as so many saltatory variations, or mutants and that they survived and secured representation in the germ-plasm, because they happened to fulfill specialized and useful functions in the life of the colony. I believe, however, that this view of the castes, at least so far as their origin is concerned, cannot be maintained, because all the available evidence points to their being merely the surviving extremes of graduated and continuous series of forms, the annectant members of which have suffered phylogenetic suppression or extinction."

Thompson (1917) in commenting upon the phylogenetic origin of termite castes makes the following statement:

"The manner in which these castes have arisen in the individual life cycle is perhaps indicative of the way they arose phylogenetically. The phylogeny of *Leucotermes* may have begun in a primitive ancestral reproductive type with a tendency to throw off sterile or worker variations, perhaps mutants. This tendency became fixed in the species, and the generalized reproductive type and the generalized worker-soldier type occurred side by side in every generation. Both types still kept the tendency to vary, or mutate; as time went on, the generalized reproductive type threw off the more specialized adults of the second form, with short wing pads, etc., the type itself continuing as the adult of the first form, with ancestral structure and habits. If the third reproductive caste, with no wing pads, is a true caste, it may be accounted for, according to this hypothesis, as a second mutant from the ancestral parent reproductive type. . . . Still later, the generalized worker-soldier type differentiated or split up into the highly specialized soldier caste and the primitive worker caste which more nearly resembles the parent form. Both soldier and worker may manifest their inherent variability by occasional fertility."

Imms (1919) discusses the phylogenetic development of the castes at some length and offers many interesting theories to explain the facts. Following are quotations from this important contribution:

"Certain phases of polymorphism among social insects appear to me to admit of a relatively simple interpretation in terms of the Mendelian theory of heredity. In the present instance it is not my intention to attempt to explain the phenomenon in any insects other than the Termitidae. Among the Hymenoptera it is an attribute of the female sex, and has apparently evolved along somewhat different lines. According to the usually accepted biological criteria, the characters of the ancestral type among the Termitidae are exhibited, in their least modified form, in the winged males and females. The soldiers betray obvious specialisations on the one hand, and indications of degeneration on the other. For this reason it is probable that the primitive Termites consisted solely of winged males and females, and exhibited at first no manifestations of a communal life. The prototype of the worker can be explained as having risen as a mutation of the nymph stage, and characterised by the absence of wing rudiments, and the possession of a markedly larger head and jaws than those of the race from which it sprang. Natural selection would then come into play and favour the increased development of useful characters, and the degeneration of certain others, along lines already suggested by Weismann (*loc. cit.*). It is probable that the soldier caste similarly arose by a further mutation or series of mutations. The fact that transitional forms, intermediate in character between the soldier, worker, and winged castes, are practically unknown argues in favour of these mutations being inherited according to the laws of Mendelian segregation. . . .

The presence of worker-like individuals in *Archotermopsis* has a direct bearing upon the origin of the worker castes among Termites. . . . I consider that they exhibit the first step in the evolution of the worker caste, a conclusion which, if correct, is in full accordance with the presence of other primitive features associated with *Archotermopsis*. At the same time they afford a clue as to the possible origin of the worker, which appears to have arisen as a mutation of the nymphal stage and not of the winged adult. . . .

. . . . In its general morphological features the worker is clearly a less modified form than the soldier. Whether the former is phylogenetically the older type or not is uncertain. . . . At present, . . . we have insufficient evidence to decide whether the soldier mutation arose *de novo* from the nymphal form, or secondarily as a further offshoot from the worker."

Imms makes an attempt to compose a genetic formula on the basis of several allelomorphs expressing themselves collectively in the winged sexual adults and includes the further development of polymorphism among the sterile castes in the explanation.

I do not find it possible to make Imms' genetic formula agree with known facts. He postulates the mating of two heterozygous winged sexual forms which results in the many combinations of factors which might determine the various castes. Among the progeny, however, appear homozygous winged sexual forms which if mated together would produce nothing but homozygous winged sexual forms. This hardly conforms to the known biological observations on termites. It might, however, still be possible to construct a theoretical genetic formula with the introduction of lethal factors. Snyder (1925) has suggested the presence of lethal factors.

On the basis of these admitted speculations, Imms arrives at the following conclusions:

"The Mendelian inheritance of mutations offers a possible solution of polymorphism among Termites, and more especially affords an explanation of: (1) The absence of intermediate forms between the castes; (2) the constant occurrence in each generation of castes which themselves have become sterile; (3) the occurrence of dimorphism and trimorphism among workers and soldiers; (4) the occasional presence of wing rudiments in members of sterile castes, and the occurrence of 'nymph-soldiers' and 'nymph-workers'."

Snyder (1920) summarizes his paper on 'The colonizing Reproductive Adults of Termites' as follows:

"It seems to the writer not unreasonable to conclude that the second and third reproductive forms, as well as the intermediates, in termites are mutations. They, so far as is known, breed true to type; in this case, then, all castes are mutations from the parent first form, and a plausible explanation for the phenomenon of polymorphism is afforded."

Thompson's (1922) posthumous paper on the castes of *Termopsis* contains at the end a discussion of the theory of the origin of polymorphism from which the following quotations are taken:

"Thompson and Snyder (1919), attempting to answer the question of the mode of origin of the termite castes, suggested that the castes might be interpreted either as a series of fluctuating variations or as mutations "comparable to the series of mutations found in *Drosophila*." To-day, the writer, influenced by the recent work of Morgan and his school, especially by their interpretation of the genetic behavior of *Oenothera lamarckiana*, believes that termite castes should be interpreted as comparable to the offspring of *Oenothera*, as arising by segregation from a heterozygous parent form. In modern terminology, therefore, the termite castes are not mutants, in the sense of the progeny of *Drosophila*, arising once for all from a mutating parent, and then breeding true, but are rather segregants, in the sense of the offspring of *Oenothera lamarckiana*, arising generation after generation by splitting and recombination of the genes of a heterozygous parent form. My views on this point therefore, are in general agreement with those of Imms, except in the use of the term mutant, which cannot to-day be applied with exactness to the recurrent termite castes.

With another theoretical point advanced by Imms I am unable to agree. . . . Imms' statement, that workers may have arisen as mutations of the nymphal stage, and not of the winged adult, has a flavor of the neoteinic or 'substitution' idea, which seems in disharmony with his other views and which I am unable to support."

Whether these castes have arisen by fluctuating variations, mutations, or as segregants still remains a matter for speculation. However, we may gain insight into the courses along which the castes have developed phylogenetically by a study of the polymorphism found in living termites.

It seems obvious that at least the second form reproductive type originated phylogenetically from the first form because of the presence of wing buds, compound eyes, and ocelli. Whether the third form originated from the first form, second form or worker, is not quite so obvious. As the workers are sterile and are lacking in groups that possess the third form, however, it is probable that the origin of this caste lies in the first or second form.

As far as is known, the *Termopsinae*, *Stolotermitinae* and *Kalotermitinae* lack workers, but possess well developed soldiers and the three reproductive castes. References to workers in these groups are probably all erroneous as indicated by the careful work of Thompson (1917, 1919, 1922), Imms (1919) and others. A true adult worker caste may, however, be present in *Mastotermes* and *Hodotermes*. These two genera, however, are socially more highly special-

ized than the *Termopsinae, Stolotermitinae,* and *Kalotermitinae,* and if, after careful investigation, an adult worker caste is found to be present, it is conceivable that it has been developed phylogenetically in a different manner from the worker of the *Rhinotermitidae* and *Termitidae.* The worker caste would thus be polyphyletic. Otherwise, one must assume that the worker caste in the *Termopsinae, Stolotermitinae* and *Kalotermitinae* has been lost secondarily. This latter view is held by Claude Fuller, but the evidence to support it or refute it is very meager. The presence of a true worker caste in the most primitive termites would indicate that this caste had been secondarily lost in the higher forms.

Although *Mastotermes* is generally considered the most primitive termite from a morphological standpoint, its social life is by no means as primitive as that found in various genera of the *Kalotermitidae* (*Archotermopsis, Termopsis, Kalotermes*) and even in morphological characteristics, *Archotermopsis* is more primitive in some respects. Imms (1919) makes the following statement:

> "*Mastotermes* is remarkable in that it possesses a well developed anal lobe in the hind pair of wings, the tarsi have five complete joints, ocelli are present, and sub-anal styles occur in both sexes. These primitive characters are wanting in *Archotermopsis.* On the other hand in the possession of 6–8 jointed cerci, longer sub-anal styles and reniform eyes in the winged forms, the latter genus retains generalized features which are not found in *Mastotermes.* These two genera are to be regarded as divergent offshoots from the primitive Isopteran stock."

An additional primitive character in *Archotermopsis* not found in *Mastotermes* is the presence of compound eyes in the soldier. *Archotermopsis* also lacks the worker caste. With regard to this point Imms (1919) says:

> "During a tolerably intimate acquaintance with this species in India for nearly two years, I never came across any true workers, and no evidence is forthcoming proving that such a caste exists."

Even if a true worker exists in *Mastotermes,* a point which needs careful verification, it would be difficult to believe that this caste had been lost secondarily in *Archotermopsis* which shows certain more generalized features than *Mastotermes.*

I hold the opinion that the soldier caste has developed phylogenetically from the first form reproductive adult and not from the worker as suggested by Thompson (1917). The evidence for my opinion is found in the following facts:

1. Primitive soldiers are sometimes fertile or approach fertility (Heath, 1903; Imms, 1919; Thompson, 1922).
2. Soldiers are often found with wing buds which may be pigmented in the *Kalotermitidae.* None with wing buds have ever been found in the higher termites, however. If the soldiers evolved from the third form, how could they possess wing buds?
3. The primitive soldiers always possess small compound eyes and may even possess traces of the lateral ocelli in some cases.
4. Soldiers are found among all the primitive termites, even where the worker is lacking. The only genus which lacks soldiers (*Anoplotermes*) has obviously lost them secondarily as all its close relatives possess soldiers.

It has previously been thought (Snyder, Banks & Snyder, 1920) that the soldiers are probably specialized workers. Miss Thompson has also stated in her correspondence with me that "the worker is evidently more primitive (phylogenetically) than the soldier." These views are probably the result of the accepted views on the phylogenetic origin of the soldier caste in the true ants. In the *Formicidae* the soldier is undoubtedly a specialized worker and is absent in the primitive ponerine ants.

Now the question arises as to the origin of the worker. Did it arise from the nymphs of the reproductive types as found in the *Kalotermitinae* as suggested by Imms (1919)? I believe the evidence points in another way.

In the first place, Thompson (1917, 1919) finds two types of nymphs at the time of hatching, the sterile prototype and the fertile prototype. This even extends to the *Kalotermitidae* concerning which she (1919) makes the following statement:

> "In size, shape and general external appearance these newly hatched nymphs (*Calotermes* n.sp.) are all alike, but, as in the genus *Reticulitermes*, they are separable by means of internal structures into two types: (a) nymphs with a large brain that almost fills the cavity of the head, large sex organs, and a white dense abdomen, the reproductive or fertile type; and (b) nymphs with a smaller brain that does not nearly fill the head cavity, smaller sex organs, and a transparent abdomen, the soldier (the worker caste is lacking in the genus *Calotermes*), or sterile type."

These same results are obtained from the study of *Termopsis*, *Cryptotermes*, and *Neotermes*, all belonging to the *Kalotermitidae*. In the higher termites (*Rhinotermitidae* and *Termitidae*) the sterile type and reproductive type are still found, but the sterile type not only develops into soldiers, but also into workers. This fact in-

dicates that the worker has not arisen phylogenetically from the reproductive castes, at least in the *Rhinotermitidae* and *Termitidae*, but is more closely related to the soldier.

Thompson and Snyder (1920) point out close morphological similarities between the third form reproductive type and the worker, but considerations in the following paragraphs seem to preclude the possibility of the worker originating from the third form reproductive caste.

The worker also shows no characteristics which link it to the reproductive castes that are not also possessed by the soldier at some stage in its development. No thoroughly verified case of fertile workers or workers with wing buds has ever been described. Silvestri (1901) says he found a number of workers of *Termes* (=*Microcerotermes*) *strunckii* with well developed reproductive organs. A careful anatomical study would be necessary before the exact caste of these individuals could be thoroughly established, however.

Further evidence of the close relationship of the workers and soldiers is seen in the development of *Nasutitermes* (*Constrictotermes*) *cavifrons* described in the preceding pages, where a soldier of one of the most highly specialized living termites passes through a worker stage which is even socially functional. If the worker has originated phylogenetically from any of the reproductive types, this ontogenetic development of the soldier would be very difficult to explain providing we accept the conclusion expressed in the preceding pages that the soldier is the most primitive sterile caste.

If the soldier is the more primitive of the sterile castes, as the facts lead me to believe, and if the worker has not developed from any of the reproductive castes, the only conclusion left for us to make is that the worker has developed from the soldier caste. The facts lead me to further qualify this statement by saying that the worker is probably a mature caste which seems to have developed phylogenetically through the specialization of soldier nymphs before they had attained the development of the mandibles and head which is characteristic of the mature soldier. This accounts for the fact that the workers resemble the imago more closely in their mouth parts and shape of head than they do the mature soldier. The young soldiers in the early stages of their development also resemble the imago in these respects.

Before this theory of the phylogenetic origin of the worker caste can be applied to all termites, careful investigations of the

development of the worker caste in *Mastotermes* and *Hodotermes* must be completed.

The two sterile castes, workers and soldiers, after their establishment in the phylogenetic series, have further differentiated, the workers dividing in some cases (*Syntermes, Bellicositermes, Nasutitermes, Microcerotermes*) into two or more types which are mature as far as we know. The soldiers have evolved other types such as the minor soldier of *Rhinotermes, Bellicositermes, Acanthotermes,* etc., and also the nasuate soldier has developed from the mandibulate type through intermediate stages such as *Syntermes, Cornitermes* and *Armitermes* and after attaining the nasuate type, has still further differentiated into as many as three mature types found in *Diversitermes.* The soldier of *Constrictotermes* may conceivably have developed from one of these three soldier types, the other two, including the primitive nasuate soldier type, having been eliminated during the course of evolution.

The view that the nasuate soldier is not a true soldier but is a separate caste (nasutus) suggested by Thompson and Snyder (1919) and Imms (1919) has found its way into some recent text-books but has no facts to support it. Snyder, in a recent paper, refers to the "nasutus" as a soldier and points out the significance of the form found in the genus *Armitermes* which is intermediate between the mandibulate and the nasuate soldier.

To my mind, the most remarkable case of phylogenetic differentiation among the sterile castes of termites is found in the genus *Rhinotermes,* s.str. *Schedorhinotermes* possesses an intermediate stage in the development described below.

The facts indicate that the large mandibulate soldier of *Rhinotermes* gave rise to a minor soldier which gradually developed an elongated labrum for dispersal of the secretion of the frontal gland, and lost the large mandibles which gradually degenerated into functionless minute points. This evolution finally resulted in the establishment of two types of soldiers within the same colony, one specialized for biting, the other specialized for the emission of a defensive volatile liquid.

How could such an evolution take place when the soldier cannot reproduce and thus pass on useful variations or mutations to succeeding generations? Is it theoretically possible for one sterile caste to give rise to another in the phylogenetic series as many facts reviewed in the preceding pages seems to indicate has happened?

In order that natural selection may have influenced this evolution, it is necessary for us to assume that the parents that produce the best adapted sterile castes survive and pass on to their fertile progeny the power to produce the same types of sterile castes.

As the sterile caste must originate in the germ plasm of the fertile caste, the statement that one sterile caste originates phylogenetically from another must be modified somewhat. The set of determiners in the germ plasm which cause the production of one sterile caste would have to evolve another set of modified determiners during the course of evolution so that the original sterile caste, such as the major soldier (having itself undergone evolution), and a somewhat different sterile caste, such as the minor soldier, could be produced by the same fertile pair. This fertile pair would also possess other sets of fertile and sterile caste determiners that would produce all the other castes. If such a conception is true, when we referred to the phylogenetic development of one caste from another, we would mean that the set of determiners in the fertile forms that produced the new caste would have evolved from the set of determiners in the fertile forms that produced the more primitive caste.

Thompson (1922) disagrees with Imms' (1919) conception that one caste could evolve from the nymph of another. In my opinion there is no greater difficulty in this theory than in the theory that one highly specialized larva of, let us say, the Tricoptera could evolve from a more generalized larva or that the adult female glow-worm (*Phengodes*) could have evolved by specialization of the larva stage.

These speculations, I hope, will serve to point out the importance of further investigations of the ontogenetic and phylogenetic development of the castes of social insects, particularly cytological, genetic, and embryological studies which at present are almost wholly lacking.

Summary and Conclusions

1. A nasuate soldier nymph was found emerging from a pigmented worker-like skin.
2. Two types of fully pigmented workers can be distinguished by head measurement in the colony, the smaller of which internally shows a slightly more developed frontal gland than the larger type.
3. Both types function in the colony as workers and their food is the same.

4. The smaller of these worker types develops into the soldier and during the metamorphosis, the head is prolonged into a 'nose,' the number of antennal segments is reduced from 16 to 15, the mandibles become degenerate and functionless, the maxillary and labial palpi elongate and also the antennae segments elongate, the frontal gland enlarges into a conspicuous sac, a duct develops from the hypodermis connecting the frontal gland with the end of the 'nose' and, finally, new muscles are developed while other muscles become smaller.
5. Food does not seem to have any possible influence upon the development of the soldier at this stage.
6. The 2d form reproductive type has probably arisen phylogenetically from the 1st form reproductive type.
7. The soldiers have probably arisen phylogenetically from the 1st form reproductive type and may be considered the primitive sterile caste.
8. The workers of the *Rhinotermitidae* and *Termitidae* have probably arisen phylogenetically from the soldier nymphs which have not yet attained the specialized shape of the head and mandibles found in mature soldiers.
9. Both the sterile castes have further differentiated phylogenetically into other types, some of which have attained a high degree of specialization along other lines from the original sterile type. Two or three different types of soldiers and two or three different types of workers may be found in the same colony.
10. Speculations on the mechanism of phylogenetic and ontogenetic development of the castes of social insects serve to point out great gaps in our knowledge of this phenomenon.

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